GENECOLOGY OF *CERASTIUM ARVENSE* AND *C. BEERINGIANUM* (CARYOPHYLLACEAE) IN NORTHWEST WASHINGTON

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ABSTRACT

From principal components analyses, patterns of morphological variation were determined in and among three populations of *Cerastium arvense* and one population of *C. beeringianum,* under both field (natural) and garden conditions. The three populations of *C. arvense* occurred at near sea level, mid-montane and alpine elevations, respectively. The *C. beeringianum* population was also alpine and occurred on a serpentine substrate, as did the mid-montane population of *C. arvense.* The analyses showed considerable phenotypic plasticity in non-serpentine populations, much less in serpentine populations. There appeared to be little genetic differentiation in *C. arvense* along the elevational gradient, except for a more or less persistent cushion habit in the alpine population. The two closely related species overlapped morphologically but could be separated by variables used, especially when grown under garden conditions.

Cerastium arvense was described as "one of the most perplexing species in our range" by Hitchcock et al. (1964). They noted further that *C. beeringianum* cannot be satisfactorily separated from *C. arvense* in the high Cascades where the characteristics of the two taxa tend to merge. According to Hultén (1956) these species hybridize in Newfoundland and Labrador and are part of a large polyploid complex united by introgressive hybridization. Chromosome numbers of most members of the complex are known (Sollner 1954, Brett 1955, Ugborogho 1973, 1977). Ploidy of *C. arvense* varies but appears to be diploid ($2n = 36$) throughout the Pacific Northwest, whereas *C. beeringianum* is a tetraploid ($2n = 72$). Meiotic regularity and high pollen viability provide evidence that *C. beeringianum* is a stable allotetraploid.

Interspecific hybridization in Hultén's complex has undoubtedly been facilitated by reproductive biology. At least *C. arvense* is an obligate outcrosser that requires insect pollination for successful seed set (Ugborogho 1977); and both taxa have open, bowl-shaped flowers that provide easy access to pollen and nectar rewards by insects. The

generalist pollination strategy of the two species has been substantiated (Ugborogho 1977, Arroyo et al. 1982, Shaw and Taylor 1986).

Cerastium arvense is widely distributed, both geographically and altitudinally. In the Pacific Northwest it ranges from rocky, exposed coastlines to alpine ridges. *Cerastium beeringianum,* on the other hand, has a restricted distribution in the Northwest, occurring in a few alpine locations. The purpose of our study, then, was two-fold: (1) to examine the patterns of variation within and among geographically and elevationally disjunct populations of *Cerastium* and to ascertain the extent to which observed variation was the result of phenotypic plasticity and to what extent it is genetically fixed; (2) to confirm the taxonomic distinction of an alpine population thought to be *C. beeringianum* and to compare patterns of variation of this population to those of *C. arvense.*

METHODS

Four sites varying in climate, elevation, and edaphic conditions were chosen for study. These sites (Deception Pass, Sumas Mountain, the Twin Sisters, and Chowder Ridge) are shown in Fig. 1 and general descriptions are given in Table 1. Detailed descriptions of the climate and geology relating to the four sites are available from Moen (1962), Phillips (1966), and McKee (1972). Taylor and Douglas (1978) described the natural history of Chowder Ridge, and Kruckeberg (1969) published a detailed account of vegetation occurring on serpentine soils in the northwest, including Sumas Mountain and the Twin Sisters.

Sampling and collection. At Deception Pass, Chowder Ridge, and the Twin Sisters *Cerastium* populations were large and the plants occurred in diverse habitats. To effectively sample the variation of these populations, we positioned four widely separated, 55 m transects parallel to the slope; the sum of the transect length was therefore 220 m. Ten specimens were collected at 20 m intervals along the total transect length. Because the *Cerastium* population at Sumas Mountain was smaller and more limited in distribution, seven shorter (20–55 m) transects were established, again with a total length of 220 m. Ten specimens were also collected at 20 m intervals along this total transect length. From each of the 40 specimens collected, three mature flowers with non-dehisced anthers were selected for pollen analysis, and plants were pressed for subsequent morphological analyses. These collections were made in the summer of 1983.

Also during the summer of 1983, 40 cuttings were collected at 5 m intervals along the transects at each study site. These were propagated in a potting mixture of one part each mineral soil (taken from respective study sites), peat, and perlite. In 1984 an additional 20 cuttings were similarly collected from each study site and prop-
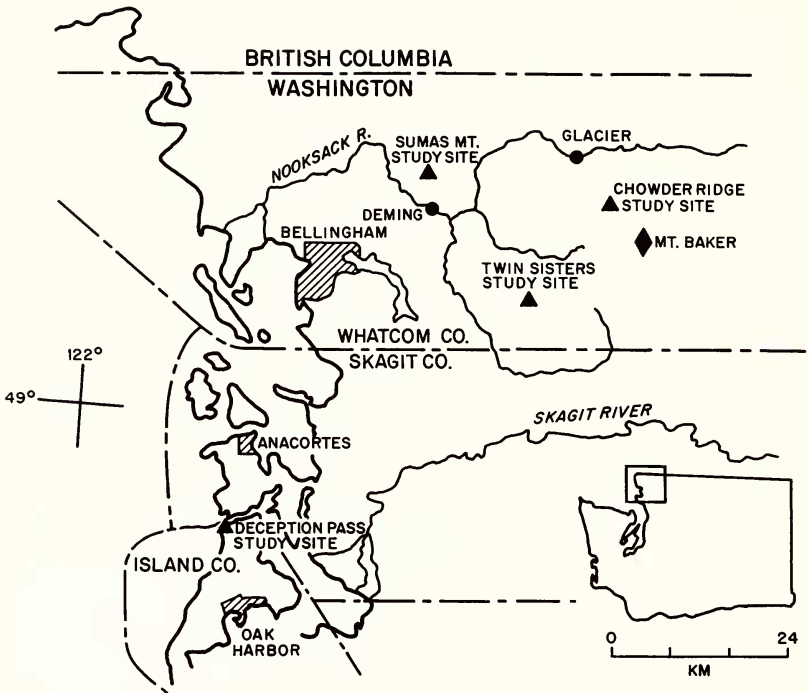
Fig. 1. Location of the four populations (triangles) of *Cerastium* studied in North-west Washington. The Twin Sisters population = *C. beeringianum*.

agated in a mixture of one part each sand, peat, and perlite. All cuttings were protected from direct sunlight until new growth was observed, then transferred to an experimental garden at Western Washington University. In June 1985, 10 mature specimens were randomly collected from each of the four transplanted populations and pressed.

Pollen analysis. The flowers sampled for pollen analysis were stored at 5°C until slides could be prepared using a technique adapted from Ugborogho (1973). Two anthers from each of the three flowers were squashed in a 1% acetocarmine and glycerine solution. The stained mounts were allowed to set for 24 hours before being examined. This enabled the pollen grains to absorb the stain and stabilize in size. Using a calibrated stage, each slide was then divided into quadrats and 25 pollen grains were observed from each quadrat. Pollen grains that were swollen and deeply stained were scored as viable. In addition, every tenth pollen grain was measured using a calibrated occular.

Morphometric analysis. Twenty-three morphologic and pollen variables were chosen for analyses. These are listed in Tables 2 and

TABLE 1. ENVIRONMENTAL CONDITIONS OF STUDY SITES.

Location	Elevation (m)	Mean annual precipitation (cm)	Topography	Aspect	Soil parent materials
Deception Pass	sea level–148	51	gentle coastal bluff to steep rock outcroppings	se.	marine sediments
Sumas Mountain	799–832	179	steep non-forested rock outcroppings	ene.	serpentine
Twin Sisters	1665–1831 (alpine)	279	steep rocky slope	nw.	serpentine
Chowder Ridge	2200–2300 (alpine)	305	steep rocky slope	sse.	marine sediments and andesite

TABLE 2. VARIABLES USED IN PRINCIPAL COMPONENTS ANALYSES. Factor loadings are given for the first and second principal components of 40 field, 40 garden, and 80 field + garden (fld + gard) specimens. Variables making a relative contribution of more than 0.5 to indicated component(s) have been highlighted. Signs of the loading values have been disregarded.

	Factor 1			Factor 2		
	Field	Garden	Fld + gard	Field	Garden	Fld + gard
Distance between bracts and first leaves (mm)	0.85531	0.76875	0.73369	0.30934	0.19163	0.45323
Length of the flowering stem (cm)	0.84327	0.88889	0.76201	0.31695	0.18310	0.52825
Length of the upper internodes (mm)	0.77374	0.89845	0.57964	0.54616	0.02423	0.66768
Mean pollen diameter	0.73230	0.26002	0.61612	0.31551	0.58208	0.42545
Number of cymes per inflorescence	0.69873	0.23644	0.61788	0.26480	0.54087	0.07718
Length of the first leaf below the bracts (mm)	0.68615	0.82621	0.60270	0.22297	0.06093	0.49596
Length of petals (mm)	0.68439	0.01570	0.67515	0.09721	0.61116	0.14408
Length of the second internodes (mm)	0.67764	0.86001	0.46378	0.60301	0.12896	0.72235
Length of pubescence on the stem below bracts (mm)	0.65416	0.17521	0.50870	0.31993	0.60825	0.42931
Width of first leaf below bracts (mm)	0.58926	0.11077	0.70397	0.60974	0.81121	0.41151
Width of bracts (mm)	0.52118	0.10492	0.66511	0.66289	0.79813	0.42235
Number of flowers per cyme	0.50590	0.69438	0.58527	0.19893	0.15764	0.36709
Length of bracts (mm)	0.49922	0.32695	0.59338	0.59825	0.50183	0.19834
Number of sterile shoots in leaf nodes	0.49479	0.63240	0.31098	0.06596	0.26307	0.45527
Length of sepals (mm)	0.47757	0.12228	0.42661	0.05385	0.61544	0.01778
Width of scarious margin on bracts (mm)	0.42967	0.53107	0.26783	0.64410	0.35616	0.64449
Length of pubescence on sepals (mm)	0.31036	0.19523	0.49227	0.14782	0.70497	0.36552
% Pollen stainability	0.19889	0.24509	0.13902	0.25684	0.37802	0.32604
Depth of petal lobes (mm)	0.18227	0.22543	0.16280	0.09695	0.09069	0.22467
Width of petals (mm)	0.18076	0.31942	0.39034	0.23087	0.30361	0.01381
Number of leaf nodes per flowering stem	0.15376	0.23292	0.12658	0.10920	0.16282	0.24841
Width of sepals (mm)	0.11708	0.05953	0.38792	0.60662	0.60119	0.36864
Standard deviation of pollen diameter	0.10512	0.02354	0.00308	0.11044	0.06818	0.07039

TABLE 3. MEAN VALUES OF VARIABLES OF FIELD VERSUS GARDEN SPECIMENS IN EACH OF THE FOUR POPULATIONS. Those values which are significantly different at a 5% level are highlighted.

Variable	Deception Pass Field	Deception Pass Garden	Sumas Mountain Field	Sumas Mountain Garden	Twin Sister Field	Twin Sister Garden	Chowder Ridge Field	Chowder Ridge Garden
Inflorescence								
Number of cymes	2.4	2.8	**2.6**	**1.7**	2.5	2.7	**1.4**	**2.9**
Number of flowers per cyme	**1.4**	**2.2**	1.3	1.7	1.3	1.5	**1.0**	**1.6**
Corolla								
Length of petals (mm)	**8.5**	**10.9**	10.1	9.5	9.9	11.4	**8.3**	**10.5**
Width of petals (mm)	**4.4**	**5.4**	4.1	4.1	4.2	4.5	4.3	5.1
Depth of petal lobes (mm)	2.3	2.8	2.1	2.5	2.8	3.0	2.3	2.7
Pollen								
% Pollen stainability	83.1	72.8	75.3	66.1	83.9	89.9	71.6	80.2
Mean pollen diameter (mm)	**36.1**	**38.1**	36.2	36.7	**39.7**	**43.5**	**33.0**	**37.6**
Standard deviation	2.3	2.1	2.8	2.8	2.6	2.5	2.4	2.6
Calyx								
Length of sepals (mm)	**4.7**	**5.3**	6.1	5.1	5.9	5.5	**4.7**	**5.7**
Width of sepals (mm)	1.7	1.8	1.6	1.7	1.9	2.0	1.7	2.2
Length of pubescence on sepals (mm)	**0.4**	**0.6**	0.4	0.3	**0.4**	**0.9**	**0.3**	**0.4**
Leaves								
Length of bracts (mm)	**3.6**	**6.9**	4.3	4.0	6.3	5.1	**3.8**	**5.3**
Width of bracts (mm)	**1.7**	**2.9**	1.6	1.8	3.3	3.6	**1.8**	**3.4**
Width of scarious margin on bracts (mm)	0.5	0.4	0.4	0.4	0.1	0.1	0.4	0.5
Length of first leaf below bracts (mm)	**8.1**	**16.6**	15.1	13.3	10.9	8.6	**8.4**	**12.8**
Width of first leaf below bracts (mm)	2.1	3.6	2.2	2.5	4.6	4.9	2.6	5.0
Number of sterile shoots in leaf nodes	9.9	8.6	6.0	6.2	3.8	3.6	9.5	5.2
Stem								
Length of flowering stem (cm)	**12.6**	**28.1**	17.2	13.7	**13.9**	**12.3**	**6.8**	**16.0**
Number of leaf nodes per flowering stem	**9.4**	**6.2**	6.7	6.3	**8.4**	**5.8**	**7.7**	**5.0**
Distance between bracts and first leaves (mm)	**25.5**	**64.5**	**8.9**	**32.8**	42.6	31.5	10.7	46.8
Length of pubescence on stem below the bracts (mm)	**0.5**	**0.6**	**0.5**	**0.4**	**0.6**	**0.8**	0.4	0
Length of upper internodes (mm)	**17.5**	**27.5**	29.3	**17.4**	**19.8**	**11.4**	7.4	**18.8**
Length of second internodes (mm)	**12.2**	**18.0**	17.4	**11.8**	11.7	**4.9**	6.2	11.8

3 and were used in principal components analyses available through Nie et al. (1983). In addition, a t-test of independent means was used to compare the intrapopulation variation between garden and field collections from each of the four locations. The significance level was established at p ≤ 0.05.

RESULTS

Transplant establishment. Between 25 and 41% of the cuttings survived transplantation. Survival rates during the several months that the plants were maintained in the pots depended on the population source and potting mixture. Plants from Chowder Ridge and Deception Pass exhibited apparent preference for soil mixtures containing sand rather than native soil. In contrast, plants from the serpentine populations fared significantly better when propagated in mixtures containing native soils.

Following transplantation from the pots into the garden, the plants readily became established and formed mats up to 83 cm in diameter by the end of the second year. During the second year the garden transplants flowered and successfully set seed. As shown in Fig. 2, the low elevation field populations flowered earlier in the season than did the alpine populations. However, garden transplants flowered simultaneously regardless of their source.

The requirements for seed germination were less uniform. Seeds from Deception Pass and Sumas Mountain transplants germinated within ca. 14 days on moistened filter paper at 5°C, whereas low germination rates were observed for alpine transplants.

Factor analyses. Analyses involving variables listed in Table 2 were used to quantify intra- and interpopulational variation, to establish relationships among populations, and to determine the extent to which observed variation was due to phenotypic plasticity. Figure 3 is a two-dimensional ordination produced from a principal components analysis (PCA) of the 40 field specimens. This analysis revealed variation within each population and overlap among populations. Forty-one percent of the variance was accounted for by the first two components. Characters that received high loading on the first component were those involving overall size, inflorescence, and pollen diameter. Characters that described bract shape, and width of the scarious bract margin received high loadings on the first and second components. Factor loadings for the 23 variables in this and subsequent PCA's are given in Table 2.

As reflected in the PCA ordination of Fig. 4, interpopulational variation was reduced in garden transplants, especially between the Deception Pass and Sumas Mountain populations. The distinction between the Twin Sisters population, which ultimately proved to be *C. beeringianum,* and other, *C. arvense,* populations was rather sharp.
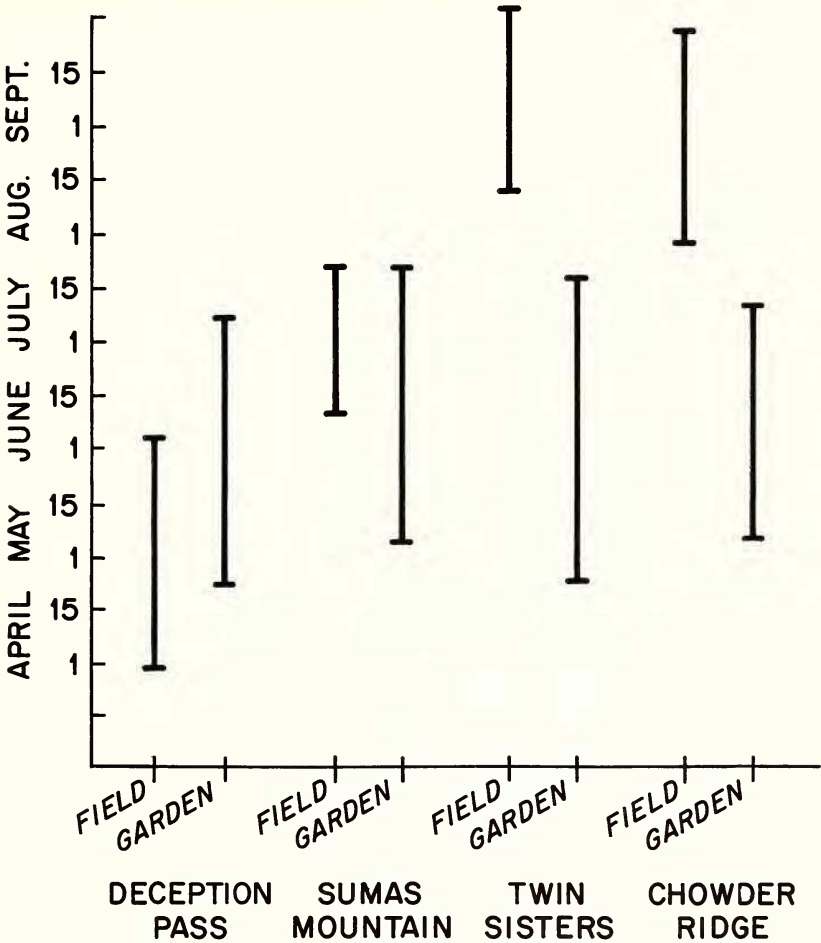
FIG. 2.   Flowering period for field populations of *Cerastium* and garden transplants.

In this analysis 35% of the variation was accounted for by the first and second components. Characters that described the overall height of the plants, the number of sterile shoots, and the width of the scarious bract margin had high loadings on the first component and therefore differed between species. Characters describing the shape of the bracts and the width of the leaves received high loadings on the second component (Table 2).
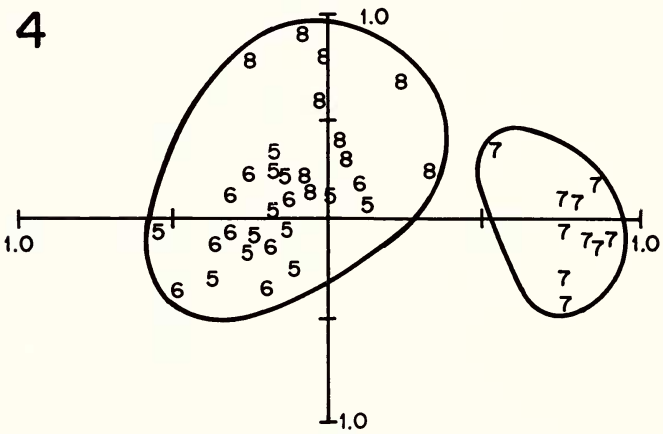
A PCA ordination of the combined field and garden data sets (Fig. 5) indicates considerable overlap among the populations. There is little differentiation between field and garden populations from the Twin Sisters and from Sumas Mountain. However, field and garden
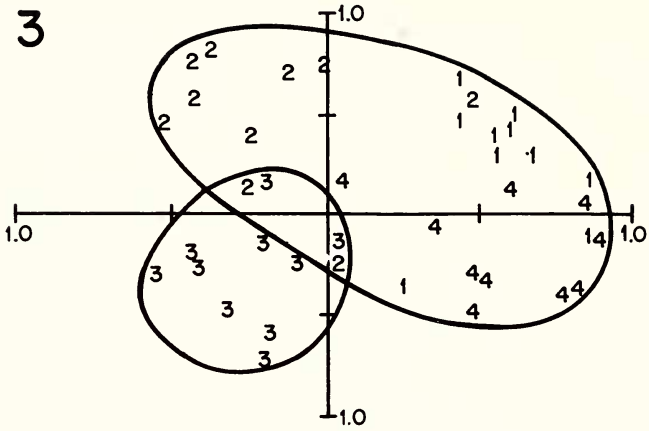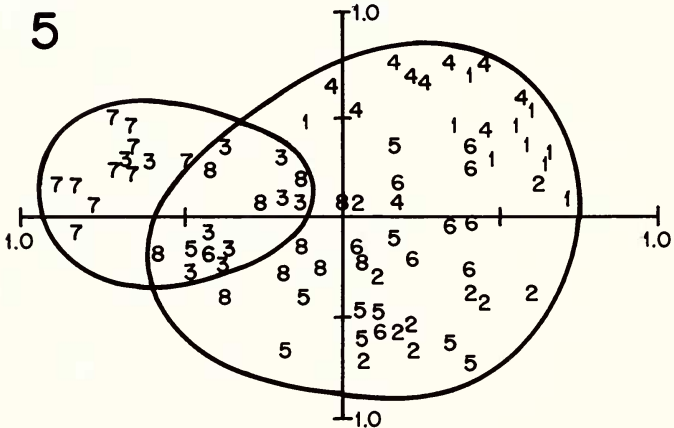
populations from the non-serpentine sites, Chowder Ridge and Deception Pass, clustered separately. This suggests that plants of the latter sites exhibited greater phenotypic plasticity. In Fig. 5 the first and second principal components accounted for 42% of the variance. Morphological complexes that described plant height, leaf width, and the inflorescence received high loading on the first component and were therefore important in separation of the Twin Sisters population and, to a lesser extent, the Chowder Ridge field population from other populations. Plant height, the width of the scarious margin on the bracts and the number of sterile shoots at the leaf nodes received high scores on the second component and thus were important in separating the field from the garden populations from Chowder Ridge and, especially, Deception Pass. Factor loadings are given in Table 2.

To determine extent of variation due to phenotypic plasticity, the independent means of variables of field and garden specimens were compared (Table 3). The number of variables that differed significantly between field and garden specimens was: 17 from the Chowder Ridge population, 14 from Deception Pass, 6 from the Twin Sisters, and 5 from Sumas Mountain. This strongly suggests that the Chowder Ridge and Deception Pass populations expressed more phenotypic plasticity than did the populations occurring on serpentine substrates. The most plastic variables were length of internodes, distance between bracts and first leaves, number of nodes, length of pubescence, and pollen diameter. These variables varied significantly between field and garden specimens from at least three of the four populations (Table 3). The least plastic variables were those describing flowers, width of the scarious margin of bracts, leaf width, number of sterile shoots, and pollen stainability.

DISCUSSION

In spite of the morphological similarity and overlap between alpine populations of *Cerastium arvense* and *C. beeringianum,* the two taxa were separable on the basis of characters used in this study. This was especially true of garden specimens (see Fig. 4). As predicted from taxonomic treatments (Fernald and Wiegand 1920, Hultén 1956, Hitchcock et al. 1964), vegetative characters were more useful in distinguishing the taxa than were the conservative floral

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FIGS. 3–5. Principal components ordinations. 3. Forty field specimens from four populations: 1 = Deception Pass, 2 = Sumas Mountain, 3 = Twin Sisters, 4 = Chowder Ridge. 4. Forty garden specimens originally from four populations: 5 = Deception Pass, 6 = Sumas Mountain, 7 = Twin Sisters, 8 = Chowder Ridge. 5. Eighty field and garden specimens (populations numbered as above); populations 5, 6, 8 = *Cerastium arvense,* 7 = *C. beeringianum.*

characters. In general, bracts subtending the inflorescence were reduced and scarious-margined in *C. arvense,* foliaceous and non-scarious in *C. beeringianum.* Leaves were narrower and longer in *C. arvense,* and axillary fascicles were restricted to the lower leaf nodes in *C. beeringianum.* However, the separation of the taxa by principal components analyses was the result of the correlation of characters and not absolute differences between the taxa, thus the difficulty of field identification of alpine forms, as noted by Hitchcock et al. (1964).

The PCA's suggest that there is little genetic distinction between the alpine (Chowder Ridge) population and low elevation populations of *C. arvense.* However, the dwarf, mat-like growth habit of the former was apparently genetically fixed. In this respect the Chowder Ridge and Twin Sisters populations were similar. The two alpine populations also exhibited more variability in terms of seed germination requirements, a common adaptive characteristic of alpine plants. Flowering times were not similarly fixed since all populations flowered simultaneously in the garden. The large amount of phenotypic plasticity in non-serpentine populations is undoubtedly adaptive and helps to explain the broad ecological tolerance of *Cerastium arvense.* It also masks genetic distinctions among populations and species. This can be seen by comparing Figs. 3 and 4; the two species were much more distinct when grown under similar conditions. The restricted plasticity of the Twin Sisters and Sumas Mountain populations was perhaps due to selective pressures and specialization associated with the peculiarities of serpentine soils. Specialization is reflected not only by low plasticity, but also by the lower rooting success in non-serpentine substrates. Similar observations were recorded by Kruckeberg (1967) in his work with serpentine plants.

As previously noted, one of the objectives of this study was to confirm the taxonomic distinction of *Cerastium arvense* and *C. beeringianum.* The selection of the Twin Sisters population was made for two reasons: it was a representative alpine population, and it was suspected to be *C. beeringianum.* As noted above, this population was morphologically distinguishable, especially under uniform (garden) conditions (Fig. 4) and it proved to be tetraploid in contrast with the diploid *C. arvense* populations (Wagstaff 1986). Our study confirms, however, that because of phenotypic plasticity, the taxa cannot easily be distinguished in the field. From our limited study, it would seem that the keys and descriptions of Hitchcock et al. (1964) and Hultén (1956) are satisfactory but that the non-plastic and correlated characters, plant height, width of scarious margins of bracts, leaf width, and number of sterile shoots, should be emphasized.

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